THE HISTORY OF A POPULATION OF LIMACINA RETROVERSA DURING ITS DRIFT ACROSS THE GULF OF MAINE

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Geographical distribution in the sea is a hydrodynamic problem, in which the flow of waters determines not only the "climate" of specific regions, but also the supply of organisms to populate these regions. A pelagic population must drift with the waters in which it lives. In contrast to littoral and terrestrial populations, there is no inherent fixity in its occurrence, save that determined by the current systems of the sea. The continuous drift of water through a given region not only raises questions regarding the maintenance of a population there (Damas, 1905; Sømme, 1933, 1934); it renders continuous observation on the natural history of the population singularly difficult, since the individuals observed at any place one day are different from those observed at the same place on another occasion.

Immigrant plankton which do not thrive or reproduce in the Gulf of Maine, but which are carried into its waters from offshore, were found by Bigelow (1926) to occur in a zone extending from the Eastern Channel along the eastern, northern and western sectors of the Gulf as though carried thither by the great cyclonic eddy which Huntsman (1924) and Bigelow (1927) have shown to dominate the circulation of the Gulf. Animals of arctic origin, *Limacina helicina, Mertensia ovum, Oikopleura van hoffeni,* and *Ptychogena lactea* were taken only in the eastern sector of this zone, apparently being unable to survive long enough to be borne further. Other immigrants, both of boreal and tropical origin, survived until carried as far as the offing of Cape Cod, but few were ever taken in the southern sector of the circuit. As his cruises were not taken with sufficient frequency, these observations yield no evidence concerning the velocity of the drift on which these invaders were borne, although its course was clearly enough indicated.

The observations on the pteropod *Limacina retroversa* Fleming [2] de-

[1] Contribution No. 196 from the Woods Hole Oceanographic Institution.

[2] We have employed the name *Limacina retroversa* Fleming because of its current use in oceanography. Dr. W. J. Clench advises me that the generic name

scribed in this paper are of interest because during the greater part of the year it has been possible to follow the history of a rather definite population as it drifted across the Gulf of Maine, noting its rate of spread, its mortality, the growth and reproduction of its individuals, and its replacement by another population of the same species.

Limacina retroversa is a boreal form occurring from latitude 50° to northern Norway off the European coast and from latitude 34° to the southern part of Davis Strait in the western Atlantic. Bigelow considered it one of the most characteristic of the permanent pelagic inhabitants of the Gulf of Maine " where its numbers depend on local reproduction and not on immigration from elsewhere." He also emphasizes the irregularity of its occurrence, an opinion with which I can agree since my observations are at some variance with his. The seasonal variation in the distribution of *Limacina* shown in Fig. 44 of Bigelow's monograph led me to suspect that its occurrence might be closely correlated with the residual drift of the superficial water, since the captures in December and January extend along the northern and western shores of the Gulf, those from February to April occur over the western and southern sectors, while records for May extend from this zone northeasterly toward the Bay of Fundy.

During the years 1933–1934 a systematic survey was made of the Gulf of Maine with the object of obtaining a more precise seasonal picture of its hydrography and biology than was available from the observations of Bigelow. Thirteen cruises were made by the research vessel " Atlantis " in the course of fifteen months, with the result that 684 hydrographic stations in the Gulf of Maine and its adjacent waters were occupied. Whenever weather permitted, a standard vertical haul was made at each station using a Heligoland larva net similar to that described by Künne (1933). The opening of the net was 143 cm. in diameter and it was made of No. 0 silk having 38 meshes to the inch. The net was drawn from a point near the bottom to the surface. The catch of each net haul was preserved and from it the *Limacina* have been separated, counted and measured.

Seasonal Distribution and Abundance

The seasonal distribution and abundance of *Limacina* throughout the year, as shown by the number of specimens caught in each haul, is presented in Figs. 1 and 2. *Limacina* was scarce in the Gulf of Maine

Spiratella has claims of priority arising from Blainville's description (*Dict. Sci. Nat.*, ix, 407, 1817). No attempt has been made to distinguish *L. retroversa* from *L. balea* Möller since the distinctness of these species is in doubt (Bigelow, 1926, p. 116).

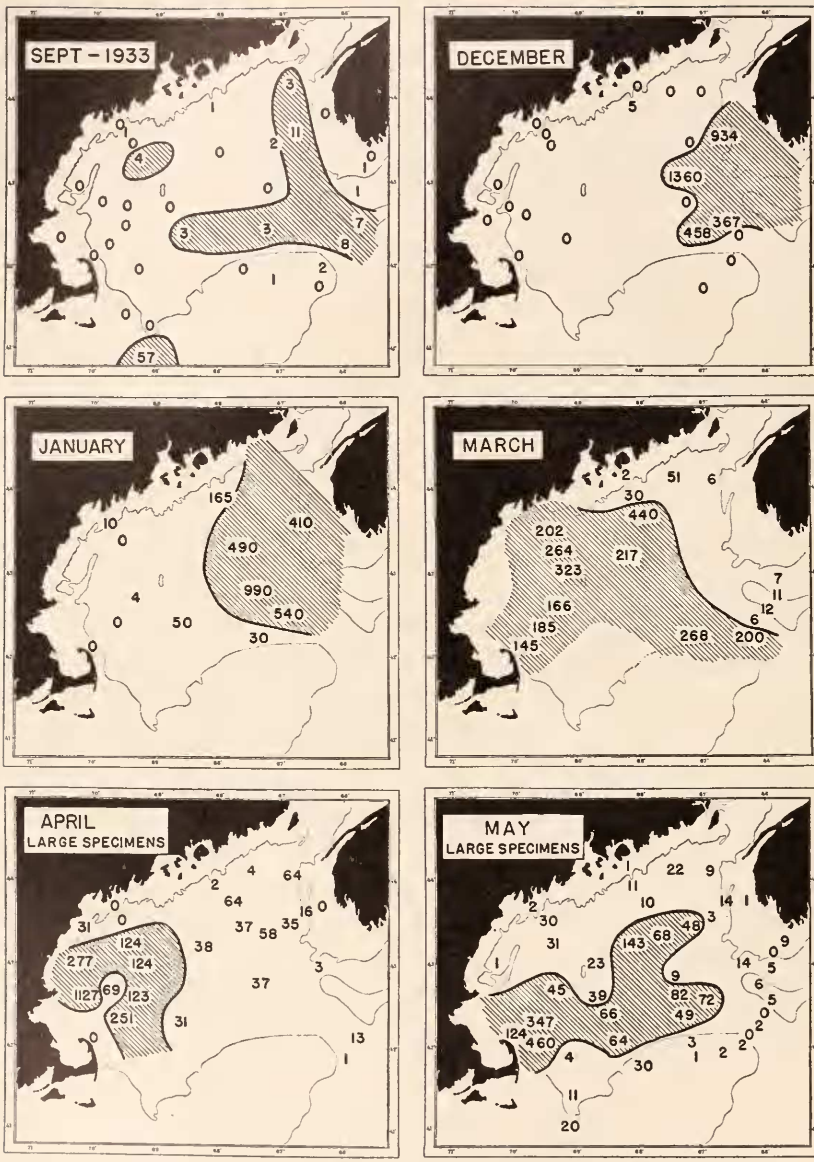

FIG. 1. Charts showing the distribution of *Limacina retroversa* in the Gulf of Maine in September and December, 1933, and in January, March, April and May, 1934. The numbers indicate the positions at which vertical hauls were made and the numbers caught per haul. The shaded area includes all hauls in which the catch was greater than the mean catch for the entire cruise. The numbers entered for April and May include only individuals attributable to population *A* as defined in text.

in the fall of 1933. A dense population of these organisms appeared in the eastern side of the Gulf in December, 1933 and spread westward during the winter. By April these pteropods are concentrated in the western side of the Gulf; the region to the eastward in which they first appeared being occupied by waters scantily populated. As the season advanced the size of the catch at each haul dwindled and the distribution became more general.

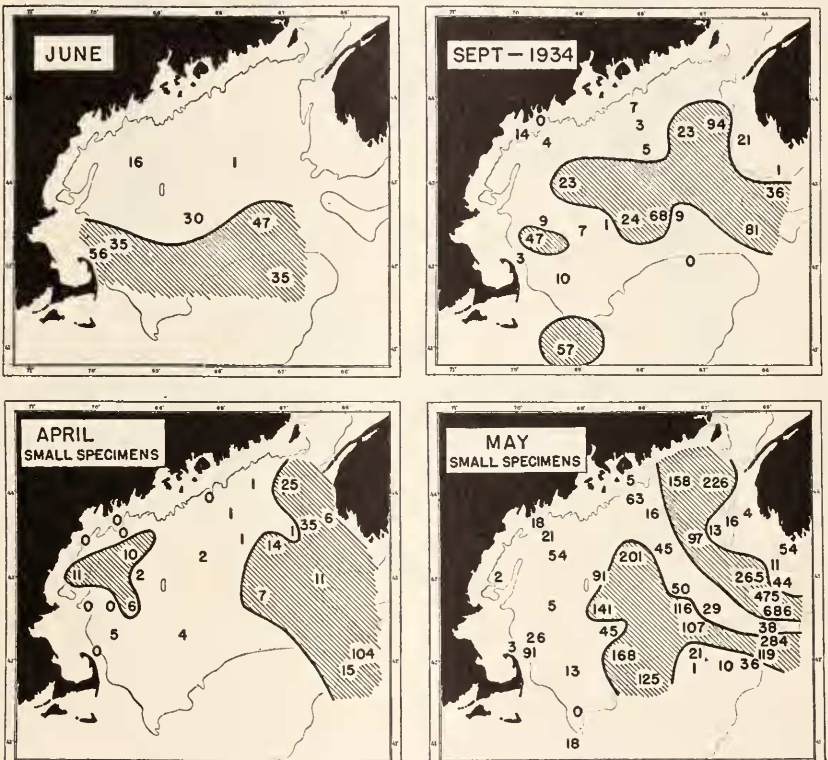

FIG. 2. Charts showing the distribution of *Limacina retroversa* of all sizes in the Gulf of Maine in June and September, 1934, and of small individuals attributable to population *B* in April and May, 1934.

These observations suggest that a huge swarm of *Limacina* drifted into the Gulf from the east in December and were carried westward by the cyclonic drift of water about the Gulf. The acceptance of this interpretation requires evidence on two points: (1) that the population moved not only in the direction but at a rate corresponding to the mass movement of the water, and (2) that a reasonable continuity exists between the population observed in December in the eastern region and that found in April and May in the western part of the Gulf.

The Circulation of the Gulf

The character of the circulation of the Gulf is adequately described by Bigelow (1927), who with Huntsman showed that the dominant circulation is a great anti-clockwise eddy around the basin of the Gulf,

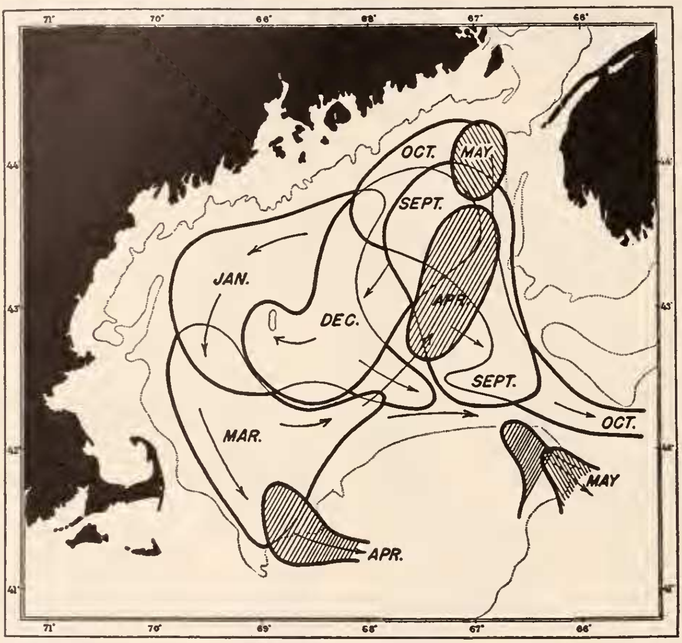

Fig. 3. Positions occupied by an area in which the salinity of the water at 50 meters depth exceeded $33^0/_{00}$ during the period from September, 1933, to May, 1934. Arrows indicate the apparent direction of drift at each period.

varying in velocity and in detail from season to season and complicated by subsidiary eddies. The great eddy receives accessions of water from the east, particularly in winter and early spring; the area of inflow being over the Northern Channel and the adjoining banks. Compensatory losses are occasioned by outflow across the Southern Channel and around the eastern end of Georges Bank. The circulation at the greater depths has a somewhat modified character owing to the confining features of the bottom contour. A report on the dynamics of the circulation of the Gulf, based on observations made during the cruises of 1933–34, is being prepared by Dr. E. E. Watson.

While our vertical hauls have given no indication of the depths at which *Limacina* occurs, it seems probable that it will be carried with the more superficial circulation of the Gulf. Bigelow (1926, p. 121) states that " the most prolific depth zone may be stated as from 20 to 25 meters down to about 80, which corroborates Paulsen's (1910) generaliza-

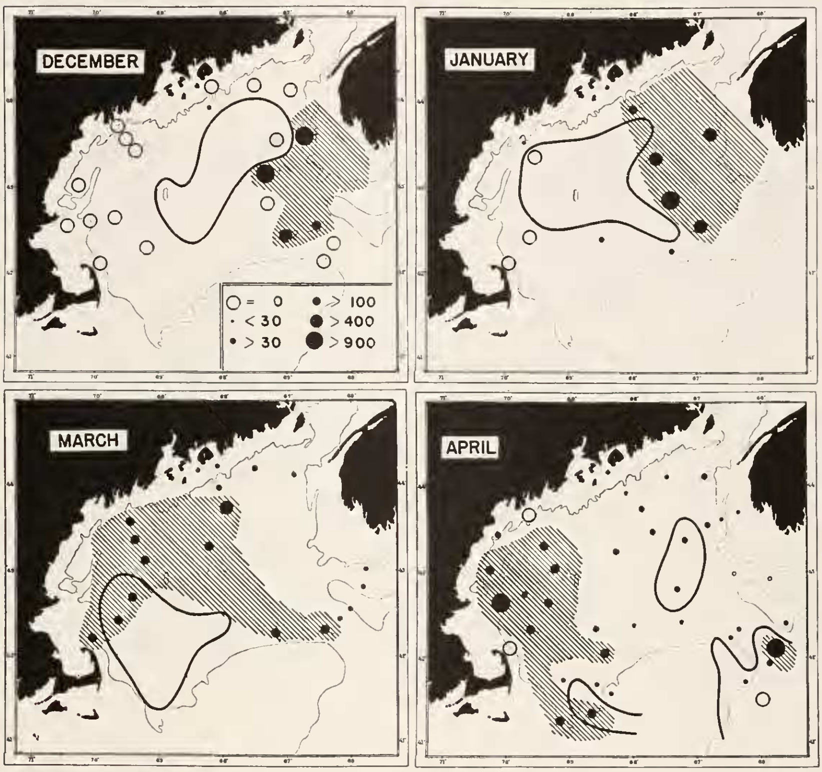

FIG. 4. Charts showing the relative positions of the area of high salinity at 50 meters depth and the distribution of *Limacina* between December, 1933 and April, 1934. The closed contours enclose the area in which $S > 33^0/_{00}$. The hatched areas include catches greater than 100 specimens per haul. The size of each catch is roughly proportional to the area of the black circles. Open circles represent hauls in which no *Limacina* were caught.

tion that *Limacina* lives chiefly shoaler than 50 meters in north European waters, though it has occasionally been taken much deeper." That the sub-surface waters actually drift with velocity as well as direction comparable to that characterizing the *Limacina* population is indicated by a study of the distribution of salinity in the upper water levels throughout the period of the survey. An extensive area characterized by salinities higher than the surroundings occurred in the eastern part of the Gulf in September,1933. Bigelow (1927, pp. 767, 768) noted a similar occurrence in 1913, 1914 and 1915. The position of this area gradually shifted during the following months, until March when it occurred in the southwestern part of the Gulf. Subsequently it could be traced with less certain continuity as it divided, apparently drifting in part out to sea, and in part in a northeasterly direction. The "saline pool" is most clearly limited in the data for salinities at 50 meters, at which depths it is enclosed by the $33^0/_{00}$ isohaline. The successive

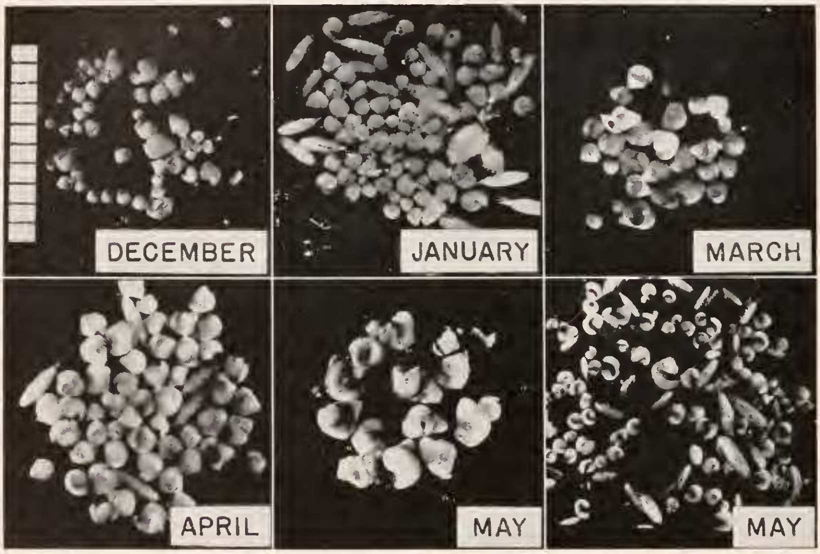

Fig. 5. Photographs of representative catches of *Limacina retroversa* taken between December, 1933 and May, 1934 showing growth. The large specimens taken in May are from the western basin and represent the size attained by population *A*. The small May specimens were taken in the eastern part of the Gulf and are attributed to population *B*. Scale, 1 centimeter divided into tenths.

positions of this isohaline are illustrated in Fig. 3, and correspond closely to the superficial circulation as deduced and illustrated by Bigelow (1927). The velocity of drift of this area, characterized by relatively high salinity, corresponds closely to that of the *Limacina* population which apparently followed close in its rear (Fig. 4). The observations on the distribution of *Limacina* and the occurrence of water of $S > 33^0/_{00}$ at 50 meters depth agree in indicating a drift during the winter period of the sub-surface waters through a distance of 150 miles in four months or at a rate of about 1.25 miles per day.

The Distribution of Size at Different Seasons

The identity of the population sampled at different periods is indicated by an examination of the distribution of size among the specimens taken. These appeared to grow larger as the winter advanced (see Fig. 5). In April and May, however, large numbers of small specimens appeared in certain catches. Since the animals taken at different times and places can only be attributed to the same population if they display a reasonable relation in size, the distribution of size among the individuals of each catch was determined. The largest diameter of the specimens was measured as they lay in random positions in a watchglass. Care was taken to avoid measurements along diameters exaggerated by the spreading of the foot as it protruded from the shell. The measurements were separated into 9 size groups of 0.3 mm. span. The number in each group was expressed as a percentage of the total catch falling within each group.

Figure 6 shows the distribution of size among all the specimens taken during each cruise. In December size distribution is homogeneous; the modal class size is 0.6–0.9 mm. with a uniform distribution of smaller and larger sizes ranging between 0.3 and 1.2 mm. In January the modal class size is the same, but the larger classes have grown at the expense of the smaller. By March a general increase in size is apparent, the modal class being 1.2–1.5 mm. and almost all specimens falling between 0.6 and 1.8 mm. The general shape of the polygon is unchanged as should be the case if the increase in size is due to uniform growth. In April the frequency polygon becomes skewed. Though the modal size is the same as in March, the larger classes have increased in number, relative to the mode, as demanded by growth. The skew is due to the appearance of significant numbers of very small (less than 0.6 mm.) individuals which were not present in the March population. In May these small specimens increase greatly in numbers with the result that the frequency polygon is bimodal. The principal modal size is now 0.3–0.6 mm., being determined by the small individuals. A secondary mode occurs between 1.5 and 1.8 mm., apparently representing the mode of the original population which determined the mode during the previous periods.

The observations made between December and May may be readily interpreted as follows. A homogeneous population of small individuals entered the Gulf from the east in December and grew continuously in size. In April a new population of small individuals appeared and by May these had increased in numbers so as to dominate the size distribution. These may represent a generation of offspring from the original

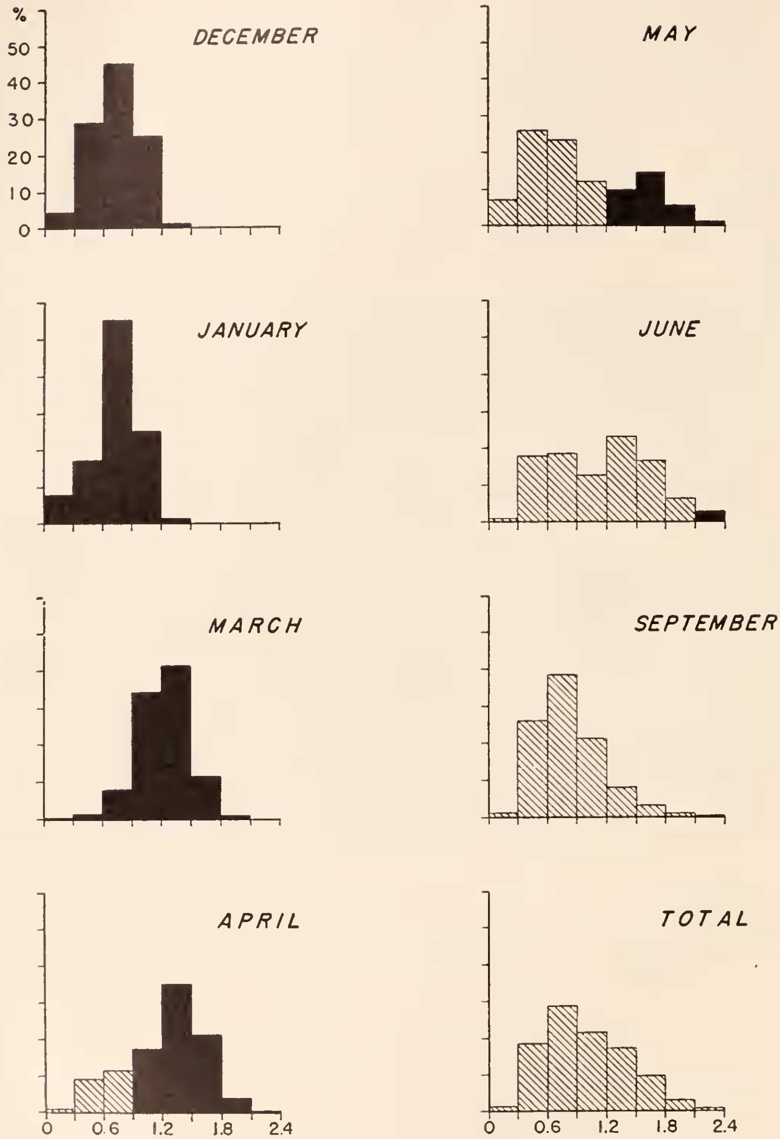

Fig. 6. Frequency polygons showing the distribution of size in the total catch of *Limacina* obtained during each cruise. The lower right-hand polygon represents the combined distribution for the entire series of cruises, corrected for variation in fishing effort. Ordinates, percentage of entire catch falling in each size group. Abscissae, size groups divided in intervals of 0.3 mm. diameter. Black areas are attributed to population *A*.

population, or an invasion of a new group from outside the Gulf, or both. For convenience we will call the original population which appeared in December the *A* population; the new population which appeared in April the *B* population.

The observations made subsequent to May are more difficult to interpret. The frequency polygon for June is again bimodal. The principal size class is now 1.2–1.5 mm. This is smaller than the mode of the *A* population for the preceding month and may be tentatively assigned to the *B* population, which may be expected to grow rapidly with the warming of the water. The largest size class, 2.1–2.4 mm., is relatively more abundant than at any previous time and probably contains the last survivors of the *A* population. A secondary mode occurs between 0.3 and 0.9 mm., which may represent a further production or a new invasion of young individuals, a hypothetical *C* population. The small specimens taken in June were caught a few miles off the coast of Cape Cod. Because of the remoteness of this position from the inflow into the Gulf, they are in all likelihood the offspring of the *A* population, which was richly represented in this region during the preceding cruise, rather than to a new invasion. Only five hauls were made during the June cruise and these all in the southwestern half of the Gulf. The data for this period are not as representative as those obtained at other times.

The scanty and scattered catches made in September, 1934 yield a simple frequency polygon with maximal size class at 0.6–0.9 mm. The distribution of size is generalized and resembles that of the combined measurements of the total collections throughout the year. Apparently during the summer growth is rapid and reproduction and recruitment of the population from without the Gulf is more or less continuous so that separate broods or populations can no longer be distinguished. Dr. Sidney Hsiao has studied the reproductive history of the collections and finds that *Limacina* produce eggs in small numbers continuously after reaching a size of 1.0 mm. It may be inferred that the offspring of one generation will vary greatly in age and after several generations their descendants may be represented by a complete assortment of sizes in which separate broods will be indistinguishable.

The Distribution of Size in the Population of Different Sectors of the Gulf

Let us return to the examination of the history of populations *A* and *B* with a view to determining whether they are actually homogeneous populations and to distinguishing whether population *B* arises through reproduction within the Gulf, or invasion from outside.

The size distribution of representative catches made in different parts of the Gulf at each period has been examined. For this purpose the Gulf has been divided into seven sectors as indicated in Fig. 7. These sectors are arranged in the order in which the non-tidal drift of water may be expected to carry a pelagic population in the circuit of the Gulf. It should be noted, however, that much water will be carried from the

FIG. 7. Chart of Gulf of Maine showing principal place names and the sectors into which the area is divided for analysis of population distribution. Contour encloses depths less than 100 meters.

Yarmouth and Mt. Desert sectors directly to the Georges sector without penetrating the western sectors of the Gulf, as Fig. 3 indicates. Representative catches made at each period in each of these sectors have been selected and their size frequency polygons are given in Fig. 8.

Figure 8 shows that from December through March the size distribution in different parts of the Gulf is homogeneous and that the increase in size noticeable in March is of general occurrence. The extension of the population westward during the winter is apparent. The

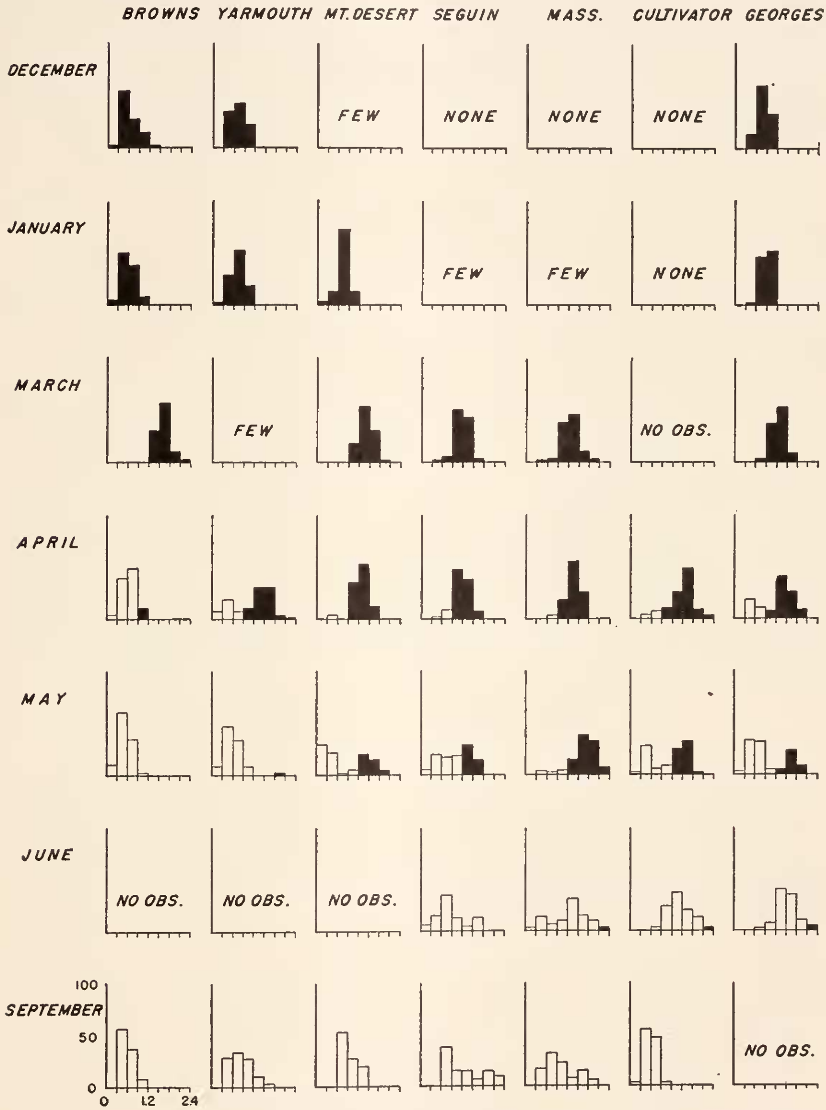

FIG. 8. Frequency polygons showing the distribution of size in representative catches of *Limacina* from each sector of the Gulf of Maine during each cruise. No hauls were made in the sectors marked *No Obs.* Ordinates, percentage of entire catch falling in each size group. Abscissa, size groups divided in intervals of 0.3 mm. diameter. Black areas are attributed to population *A*.

continuous occurrence of *Limacina* in the Georges sector is in accordance with the characteristics of the current system as noted above. In April the homogeneous *A* population appears in all the northern and western sectors of the Gulf. Small individuals representing the *B* population appear now in the eastern sectors, Browns, Yarmouth and Georges. In the outermost sector to the east, Browns, the *B* population is unaccompanied by any specimens of larger size, characteristic of the *A* population at this time.

In May the small individuals of the *B* population are much more widespread, appearing abundantly in all sectors except the most westerly, Massachusetts sector. Only small individuals occur in the stations of the Browns and Yarmouth sector. The populations of the Mt. Desert, Cultivator and Georges sectors have a mixed, bimodal character. The duplex character of the population in April or May is brought out in Figs. 1 and 2, in which the numerical distribution of individuals of different sizes is shown. Small specimens appear in numbers only in the water in the offing of the Eastern Channel in April and occur in small numbers along the course of the inflow through the Eastern Channel. In May they are generally distributed in the eastern part of the Gulf which is most accessible to inflowing water and are scarce in the western region in which the larger specimens of the *A* population are dominant.

These observations justify the belief that the *A* population represents the invasion of the Gulf from the eastward by a homogeneous population which grows as it drifts westward.

Reproduction in the Gulf

The appearance of the *B* population in the eastern sectors, unaccompanied by members of the *A* population and the extension of the smaller group westward during May makes it clear that the new population of small individuals which appears in the spring is due chiefly to a second invasion of *Limacina* into the Gulf from waters offshore and to the eastward. Whether the small individuals which occur mixed with the *A* population in several sectors are the offspring of the *A* population is difficult to decide. Dr. Hsiao finds the *A* population to contain sexually active individuals during the spring, so that offspring from this population are to be expected. On the other hand, the relative scarcity in May of the *B* population in the Massachusetts sector where the *A* population was then most concentrated, argues against the possibility that the *B* population in neighboring sectors is in any important degree the offspring of the *A* population. It is noteworthy that when the *A* population first appeared in December it was dominated by individuals of small size and no individuals of large size occurred among them. This was also true in many hauls in which the *B* population appeared in April and May. This indicates that the parental generation does not survive after breeding long enough to be caught along with offspring which have grown to diameters of 0.3 mm. or greater. This consideration also supports the view that the hauls in which large and small individuals occur together represent the mingling of populations of different origin rather than the simultaneous presence of a parental and filial generation.

Growth

Since the foregoing analysis of the collections appears to warrant the conclusion that the *A* and *B* populations are homogeneous entities,

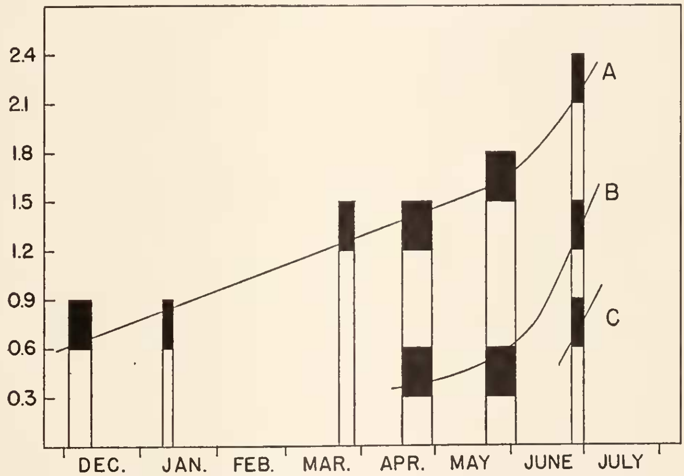

FIG. 9. Diagram indicating the increase in diameter of the modal class of *Limacina* of populations *A*, *B* and *C* during the winter of 1933–34. Ordinates, size groups divided in intervals of 0.3 mm. diameter. Abscissae, time during which collections were made. The black areas represent the modal class size of each population.

we may examine the growth rate of *Limacina* by comparing the size of the modal classes of these populations at different times throughout the year. In Fig. 9 the size of the modal class is plotted against the time the collection was made. Roughly speaking, the diameter of the *A* population doubles in about five months during the winter. At this time the temperature of the water column as a whole is below 7° C. The *B* population observed in May and June grows very much more rapidly as might be expected from the higher temperature of the surface waters at that time.

Numerical Abundance and Mortality

The *A* population is sufficiently established as a distinct and homogeneous entity and was under observation for a sufficiently long period to warrant some statistical examination of its numerical abundance. It must be realized that the number of hauls made in each cruise is insufficient and their distribution too irregular to allow great confidence in the outcome of the analysis of a matter of such complexity, but data of this sort are so rare and so difficult to obtain that one is warranted in the attempt to get the utmost out of it.

TABLE I

Statistics of the size of catches of Limacina retroversa made during the cruises of 1933–1934.

Cruises	No. of Hauls	Total Catch	Mean Catch per Haul	Per Cent of Hauls with Limacina Present	Per Cent of Hauls with Catch Greater than Mean
Sept. 2–14, '33	34	104	3	44	21
Dec. 2–11, '33	22	3120	142	23	18
Jan. 8–13, '34	12	2685	224	66	33
Mar. 21, 29, '34	18	2535	141	100	55
April 17–23, '34*—Small	24	141	6	71	33
Large	24	2575	107	84	24
Total	24	2716	113	100	23
May 21–June 3, '34—Small	44	4068	92	98	25
Large	44	1849	42	91	25
Total	44	5917	134	100	23
June 25–July 1, '34	7	220	31	100	57
Sept. 17–27, '34	26	507	20	92	20

* Two hauls made in the Eastern Channel on May 6, 1934 are included in the data for the April cruise.

We may consider that all the individuals taken in December, January and March belong to the *A* population. In order to eliminate as far as possible the *B* population individuals smaller than 0.9 mm. are eliminated from the data for April and smaller than 1.2 mm. from that for May. The *A* population cannot be identified with assurance in the June collections.

Increase in numbers can be due only to the invasion of the Gulf by new immigrants from offshore since the elimination of the *B* population precludes reproduction as a means of increase. Decreases in numbers may be due to water movements, carrying a part of the population out of the area under observation, or to mortality. Since the population first appears densely distributed at one side of the Gulf, some redistribution of density between different points of observation is to be expected as the result of lateral mixing of the water. This may be expected to result in an increasing uniformity of distribution.

Table I contains some statistics concerning the size of the catches made during the several cruises. An indication of the numerical abundance of *Limacina* in the Gulf as a whole at each period is given by the numbers in column 4 showing the average number taken per haul. Between December and January the numbers increase, after January there is a progressive decline in abundance. An examination of the distribution of *Limacina* from month to month (Fig. 1) warrants the conclusion that the invasion of the *A* population into the Gulf continues through December and January since large catches are made at these times in the region of inflow. The percentage of stations at which *Limacina* was taken (column 5) increases three-fold during this interval. The invasion appears to terminate in January, since following that period no considerable numbers of individuals referable to the *A* population were taken in the region of inflow into the Gulf. Invasion may consequently be excluded as a significant factor affecting the numbers of the population after January.

The numbers of the population decline steadily from January through May, the mean catch of large individuals referable to population *A* decreasing to less than 20 per cent of the original in four months. Significant losses are attributable to the drift of water out of the Gulf. The continuous occurrence of catches containing *Limacina* in the Georges sector, which lies in the path of outflow through the Eastern Channel, and the concentration of the *A* population in the western and southern quarters of the Gulf in April and May, where it is subject to drift outward by way of the South Channel, favor such losses.

It is probable that large losses in numbers also occur as the result of mortality. Measurements of the total volume of zoöplankton caught throughout the Gulf indicate a general mortality of about 60 per cent during the winter period.

The data in Table I indicate that the percentage of stations at which *Limacina* occurred is not less in April and May than in January. If the circulation into and out of the Gulf were rapid enough to account for the greater part of the loss in numbers, a greater decrease in the area of distribution would be expected. It may be argued that since the area of distribution does not decrease while the numbers caught per station decline five-fold, the decline is due to the death of a large part of the population. This argument, however, must be accepted with great reserve, since the lateral mixing of water may cause small numbers of animals to be carried into regions in which they did not previously occur, and will tend to enlarge the area of occurrence.

Another approach to the question of mortality may be made through an examination of the distribution of size in the catches as a whole throughout the year. In Fig. 6 the size distribution of the *total* catch is represented. This frequency polygon was prepared by averaging the percentages of the population represented by each size group during each period of collection, a procedure which corrects for the variation in " fishing effort " during different cruises, but does not correct for the irregularity of spacing of the cruises in time. The figure shows that the size most frequently caught is 0.6–0.9 mm. Smaller sizes are less frequent in part because both the *A* and *B* populations are carried into the Gulf half-grown, in part because they are more readily overlooked in sorting the catch and in the case of the smallest class, because many may pass through the mesh of the net. The larger size classes diminish progressively in their relative abundance, as would be expected if the population is subject to continuous mortality. The mode of the *A* population is 0.6–0.9 mm. in January, 1.5–1.8 mm. in May. Specimens of the latter size occur about one-third as abundantly as the former in the catches as a whole. This suggests a mortality of about 66 per cent in the time taken to grow from the former to the latter size, during four winter months. Such statistics, however, are not very convincing since the smaller classes are recruited by invasion and the chance of loss by drifting out of the Gulf increases with time, as does the size of the individuals of the population.

Lateral Mixing

The horizontal mixing of water masses, which has recently attracted the attention of hydrographers, may be expected to have consequences of importance in determining the distribution of organisms. If attention is limited to the consequences of steady residual currents, one can only conclude that the pelagic inhabitants of a region such as the Gulf of Maine which is the seat of a cyclonic eddy must be constantly washed away by the flow of water through it. The rise and decline of the *Limacina* population which we have observed supports this conclusion. The existence of lateral mixing, if of considerable extent, should tend to diminish the tendency of residual currents to transport all of the pelagic population out of such a region. By the transport of a part of the population backstream, or around and across the vortex of an eddy, an opportunity would be afforded for the endemic occurrence of the population in spite of the continuous drainage occasioned by the residual currents.

The effect of lateral mixing must tend continuously to make the distribution of the population more homogeneous. After the introduction of a limited water mass containing a rich population into a large unpopulated region, if lateral mixing alone were in operation one would expect the limits of the populated waters to become less distinct and the distribution to become more general. If samples were taken at random at any time during the mixing process, at first a limited number of samples would contain numbers far in excess of the mean value for the collections as a whole, and the remainder would contain small numbers or none at all. As mixing proceeds, the poorly populated waters would become enriched at the expense of the densely populated regions. In both regions the density of population would change in the direction of the mean population for the entire region and eventually the entire distribution would assume a random character in which the modal population density would correspond with the mean. At this point half the samples would contain more than the mean number, and an equal number less than this value. Subsequent mixing would tend only to diminish the variation of the numbers secured in the different samples.

The catches of *Limacina* have been examined for such evidences of lateral mixing. Examination of the distribution of the population shown in Fig. 1 indicates that the populated region was sharply delimited in December—no *Limacina* occurring in regions immediately in advance of the populated waters. In January moderate catches were made in regions well in advance of the main population, suggesting a gradual disintegration of the boundary zone by lateral mixing. In March the area of intense population covers more than half the Gulf and at the same time the numbers present at each station have diminished and become more uniform as required if lateral mixing is in effect. The same tendencies continue in April and May and are particularly evident when the distribution of small specimens (population B) is compared. While previous to March less than half the hauls have contained more than the mean catch for the Gulf as a whole, by March at least half the hauls are of this size—as required by random distribution. One feature of the distribution of large specimens in April and May is of particular interest. In the east central part of the Gulf, on the line between Cashes Ledge and Yarmouth, Nova Scotia, the catches of large specimens are on the whole greater in May than in April in spite of the fact that some mortality is doubtless occurring during this period and the movement is contrary to the expected drift of the water.

As a further test to see if the distribution of population is becoming more homogeneous, the catches have been grouped into classes according to the number taken per haul and the number of catches in each class has been expressed as a percentage of the total number of catches made during the cruise in question. The result is presented in Fig. 10. The left-hand diagram shows the result when the size of the catch is noted

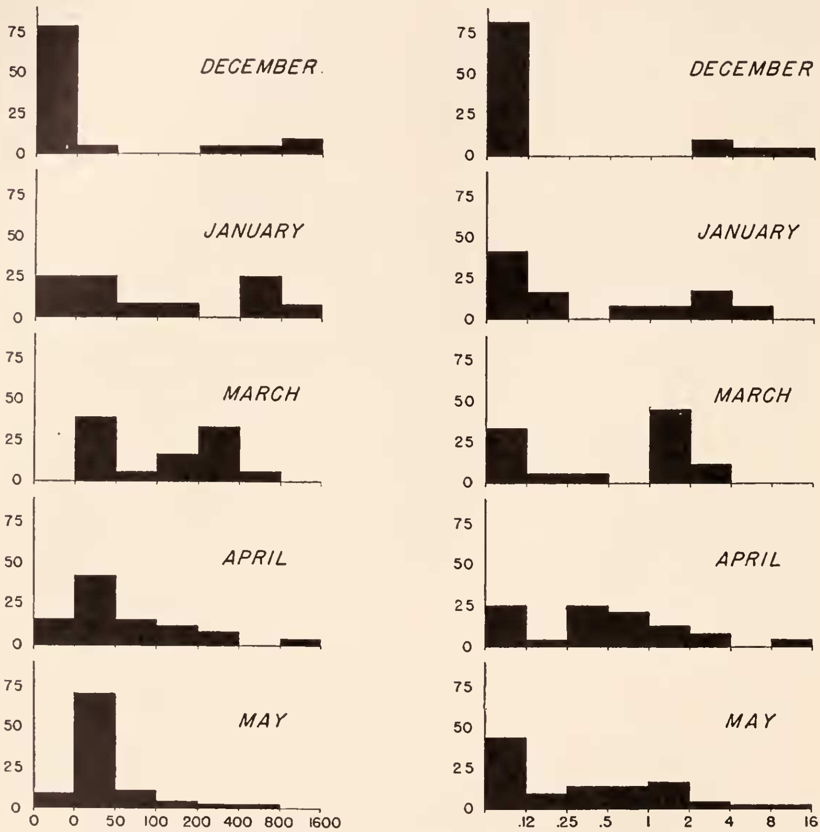

Fig. 10. Frequency polygons showing the distribution of catches of different numerical abundance among the total number of hauls made during each cruise. Ordinates, percentage of entire number of hauls yielding catches of each size. Abscissae, left-hand diagrams, size groups divided in intervals according to number caught in each haul; right-hand diagram, size groups expressed as multiples or fractions of the mean catch per haul during each period.

numerically (and assigned to classes which for convenience increase in geometrical progression). The right-hand diagram represents the same data arranged in size classes which increase as multiples, or decrease as fractions, of the mean population of the region as a whole at the period of collection. The latter procedure eliminates the effect of losses through mortality. Both diagrams indicate the complete heterogeneity of the samples in December and January and the progressive approach of both the smaller and larger catches toward the mean value which reaches its culmination in April and May.

Actually the situation observed is complicated by the drift of the population across the region and by the invasion of the eastern part of the Gulf by water poor in *Limacina* of population *A* in March and April. This inflow tends to decrease the homogenity of distribution and accounts for the increase in the proportion of catches in April and May which contained few or no *Limacina*. It also explains why the percentage of hauls in which the catch was greater than the mean diminished in the months subsequent to March. These tendencies during April and May at least make it clear that lateral mixing is not sufficiently great to obliterate the effect of the residual current in depleting the *Limacina* population of the eastern portion of the Gulf.

Because of the impossibility of separating the effects of mortality and of losses and gains through the residual movement of the water into and out of the Gulf from the apparent effects of lateral mixing, any attempt to evaluate the extent of the latter has been abandoned. Because of the great influence which such mixing would have in enabling a population to maintain itself in a region from which the residual current would constantly tend to remove it, it seems desirable, however, to emphasize the possibility of such mixing and to indicate the way in which it appears to manifest itself.

Discussion

The evidence seems definite that the population of *Limacina* which occurred in the Gulf of Maine in 1933–34 was not endemic, as Bigelow thought, but owed its origin to two separate invasions of young individuals from offshore. Unlike the less successful immigrants of arctic or tropical origin, *Limacina retroversa* thrives well enough to grow to sexual maturity and perhaps to reproduce within the Gulf and to be carried in considerable numbers to all its parts. For this reason Bigelow obtained evidence which led him to conclude the species was endemic. By following the history of these populations closely, however, it is shown that neither invasion was able to maintain its numbers in the Gulf—either because reproduction was not successful or was inadequate to balance the depletion due to mortality and the drift out of the Gulf.

The two invasions consisted of dense swarms of small individuals of very uniform size, sharply separated by a period when practically no *Limacina* occurred in the region of inflow into the Gulf. The discontinuous character of these invasions no doubt accounts for the irregularity in occurrence of *Limacina* in the Gulf noted by Bigelow. Why the invasion occurs in such definite periodic swarms can be answered only by studies carried out in the waters to the eastward from which these invasions undoubtedly come.

It is an interesting question why the invading swarms are composed of individuals of such uniform size. In describing the population found in the Gulf in September, 1934, it was pointed out that animals of all sizes were mixed together and that successive broods can no longer be distinguished. Dr. Hsiao's studies indicate that the mature *Limacina* continue to produce eggs during a considerable period of growth. Yet we found evidence to suggest that the parental generation does not survive after breeding long enough to be caught along with its offspring at the time when these enter the Gulf. Dr. Hsiao has measured numerous catches of *Limacina* taken over the continental shelf between Cape Cod and Cape Hatteras. Usually these catches are composed of individuals of uniform size, just as were those which invaded the Gulf. This riddle also can be answered only by closely timed observations in the offshore areas of production.

The most conspicuous result of this study is the demonstration of the degree to which the occurrence of *Limacina* in the Gulf of Maine depends upon the circulation of its waters. Damas in 1905 raised the question: How does the plankton of a given region maintain its character in the face of the continual circulation of the currents and how does a given species persist so as to possess a special geographic distribution? He concluded that there must exist a special zone or center of production in which adults abound and reproduce successfully and that to this region circulatory currents serve to bring back periodically a proportion of the individuals which become entrained and dispersed by the continual movements of the water. The circulatory system of the Norwegian Sea subsequently described by Helland-Hansen and Nansen (1909) appeared to supply just such a mechanism as was required to account for Damas' observation of the production centers of copepods in that region. Sømme (1933, 1934) has shown how such centers of production are established for *Calanus finmarchicus* and *hyperboreus* in the deep waters of the Norwegian fjords in winter, and has elucidated the mechanism which results in the release of the organisms from these regions at the time of reproduction. The observations on *Limacina* have not revealed the presence of a center of production in the Gulf of Maine. They point to the existence of such regions offshore to the eastward and are of interest rather in telling something of the fate of these animals, entrained in the movement of water, which are carried away never to return, yet for a while to occupy an important rôle in the ecology of other regions. Behind the geographical distribution of each species of plankton there must be a complex balance of biological and physical factors. Of the latter, flow of water appears to be paramount; its consequences too frequently neglected.

Summary

A population of small specimens of the pteropod, *Limacina retroversa,* appeared in the eastern part of the Gulf of Maine in December, 1933. From collections made during the following 9 months information was obtained showing that the population was a homogeneous one, that its members grew to maximum size in 5 months, declining in numbers as they did so.

A second population of small individuals appeared in the Gulf in late spring, originating chiefly from offshore, but possibly in part being offspring of the original population. These were unsuccessful in maintaining their numbers throughout the summer.

In addition to the information on the life history of *Limacina,* the data indicate the rate of drift of the water in its circuit of the Gulf. It supplies also suggestive information on the dispersal of organisms through the lateral mixing of water. It emphasizes the dependence of pelagic organisms upon the current systems of the ocean and the difficulty involved in maintaining a permanent population in any one locality.

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